

SCROLL COPROLITES FROM THE SILURIAN OF IRELAND AND THE FEEDING OF EARLY VERTEBRATES

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ABSTRACT. The morphology of scroll coprolites from the post-Llandovery Silurian of Louisburgh, Co. Mayo, Ireland is described. The coprolites occur within relatively fine-grained laminites along with the anaspid agnathan *Birkenia elegans* the dermal scales of *Loganellia*, and the enigmatic '*Glauconome*'. Such a faunal association also exists in the Midland Valley of Scotland. The significance of detritus as a nutrient source and the evolution of particulate feeding among the early vertebrates is examined. By association, *Birkenia* and/or *Loganellia* appear to be the most likely producers. The coprolites in the present study are the oldest known vertebrate spiral coprolites, and the first scroll coprolites to be associated with what are at present considered to be agnathans. The coprolites represent evidence for the early development of valvular intestines, of which the scroll valvular intestine now appears to be the more primitive. These coprolites also provide some of the first definite indications that particulate feeding was of significance among early vertebrates.

IN 1986 in Louisburgh, Co. Mayo, on the west coast of Ireland, a number of small elliptical pellets were discovered in post-Llandovery Silurian laminites. They were identified as spiral coprolites by Dr Douglas Palmer. The collection consists of approximately 160 coprolites, as well as many fragments and degraded coprolitic material.

The existence of coprolites was first noted in 1678 by Lister. Mantell (1822) first proposed an animal origin, which was confirmed by Buckland (1829, 1837), who assigned coprolites from the Lias of southern England to the activities of ichthyosaurs. The conclusions of both Fritsch (1895, 1907) and Neumayer (1904) were that the Permian coprolites they examined represented fossilized valvular intestines. A link between sharks and coprolites was established in 1917 by Woodward. This link was confirmed by Zangerl and Richardson (1963) with their work on the palaeoecology of Pennsylvanian black shales from Indiana. Two conflicting ideas about the formation of coprolites were published by Williams (1972) and McAllister (1985).

Although it was important to examine previous investigations of spiral coprolites, direct comparisons with the coprolites in the present study may not always be useful. Previously all spiral coprolites have been assigned to gnathostomes. The coprolites from Louisburgh are associated with what are at present considered to be agnathans. They are also the oldest vertebrate coprolites as yet described. The composition of the coprolites from Louisburgh is not phosphatic but argillaceous, which contrasts with all previously investigated coprolites whose composition is primarily phosphatic. The majority of previously described coprolites originated from spiral or transverse valves; the coprolites described here were produced by an organism which possessed a scroll or longitudinal valve. Also previously described coprolites do not appear to have suffered the same degree of flattening as the coprolites in the present study.

GEOLOGICAL SETTING

The stratigraphy of the Louisburgh area has been fully dealt with by Maguire (1989). Previously the age of this succession had been the subject of much debate. Subsequently, Palmer *et al.* (1989), by

correlation with the Midland Valley of Scotland, settled on a post-Llandovery Silurian age for the laminites. The Louisburgh/Clare Island succession, approximately 1500 m of siliciclastic sediments, resting unconformably on a metamorphic basement, includes five formations. The basal Kill Sandstone Formation, the Strake Banded Formation, and the Knockmore Sandstone Formation are composed primarily of siltstones and sandstones. The succeeding Bunnamaohaun Siltstone Formation contains the laminites from which the coprolites have been collected. The overlying Glen Pebbly Arkose Formation is composed of coarser sediments and represents the top of the succession.

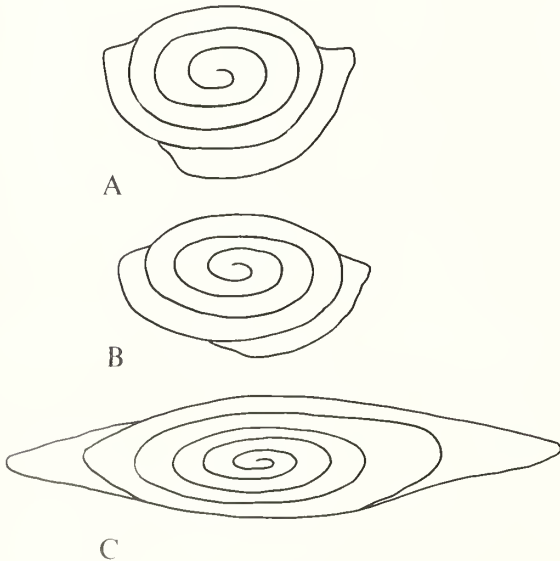
METHODS AND MATERIAL

The coprolites were examined, catalogued and measured. Suitable specimens were sectioned transversely and longitudinally. Extinction patterns were examined under plane polarized light. X-ray diffraction analysis was carried out on separately prepared samples of matrix and coprolitic material. Coprolite models were produced from modelling clay to examine the spiral coiling and deformation due to compression.

Material. Trinity College Dublin: TCD 32412, 32417, 32421, Bunnamaohaun Siltstone Fm., Louisburgh, Co. Mayo. Royal Scottish Museum, Edinburgh: T3827B, T3927, Birkenhead Burn.

DESCRIPTION

The coprolites appear as smooth, grey-brown patches of fine-grained material within the coarser matrix of the laminites. This finer grained nature is confirmed by thin-section studies. There appear to be two natural groups based on the degree of compression. One group contains coprolites which appear completely flattened and are preserved without any internal spiral structure. The second group, which has internal spiral structure (Text-fig. 1), is less numerous and the coprolites appear as bullet-shaped masses with more or less rounded ends. Exfoliation of the outer layers is often visible. Externally no spiral structure is visible in any coprolites, except for very fine sinistral striae visible on the surface of a number of them. Both groups occur side by side on the same bedding surfaces. Many coprolites occur as part and counterpart. All the coprolites display random orientation within the laminites.



TEXT-FIG. 1. Drawings of transverse sections of three scroll coprolites: note the more flattened appearance of the Irish specimen. A-B, T3827B, Birkenhead Burn, Scotland, $\times 10$. C, TCD 32421, Louisburgh, Co. Mayo, Ireland, $\times 30$.

A number of the more suitable three-dimensional coprolites were serially sectioned, perpendicular to the longitudinal axis. The sections appear as simple, continuous dorsoventrally compressed spiral coils around a central axis (Text-fig. 1c). The number of whorls varies from 4 to 6 but is typically consistent within each coprolite.

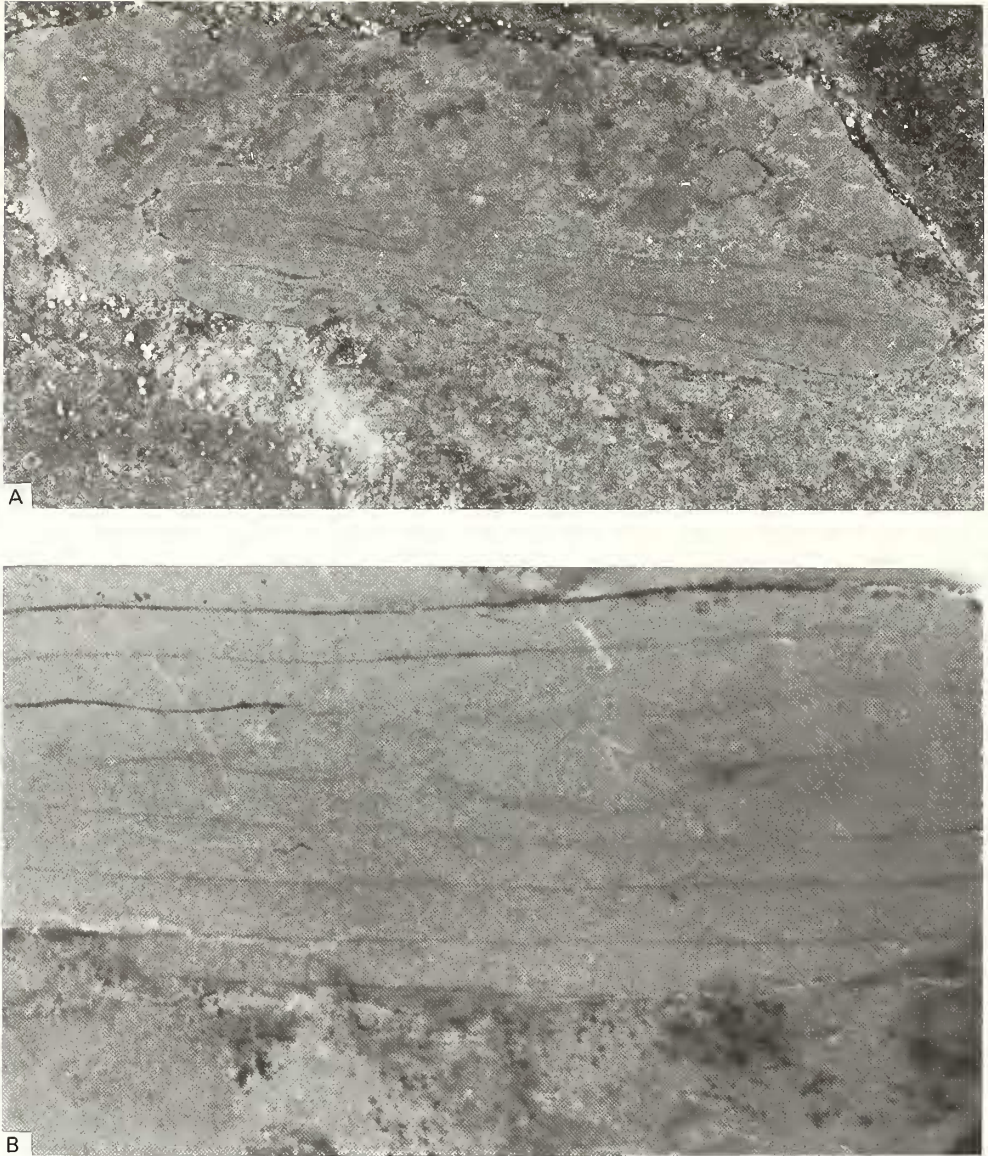


TEXT-FIG. 2. Transverse section of a scroll coprolite, TCD 32421, from Louisburgh, Co. Mayo, Ireland, $\times 45$. This section, viewed under polarized light, shows the characteristic flattened appearance, the internal spiral coil, extinction of opposite quadrants, and the contrasting grain size between coprolite and matrix, typical of the coprolites sectioned.

The second most striking feature of these sections is the extremely fine-grained nature of the material in the coil. The contrast in grain size with the matrix suggests that some degree of selection occurred prior to defaecation (Text-fig. 2). The longitudinal sections also display this fine-grained texture (Text-fig. 3), but the most noteworthy feature of these sections is the scroll-like coiling consistent with the internal morphology of scroll coprolites (Text-fig. 4). The importance of obtaining longitudinal sections is stressed by Jain (1983). Of all previous investigators, Jain alone describes what he claims to be scroll coprolites; all other authors describe spirally-coiled coprolites.

DETRITUS AND FEEDING

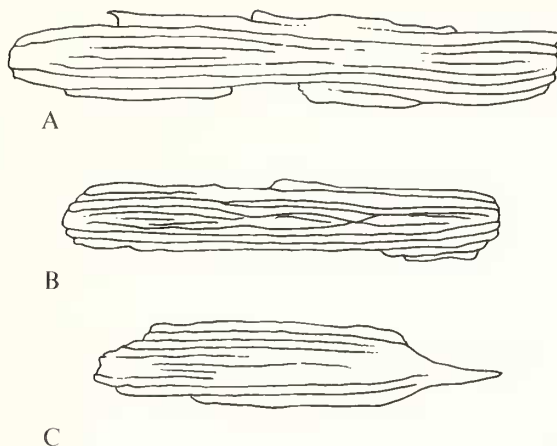
Many of the previous reviews of early vertebrate feeding appear to be in general agreement that sediment or deposit feeding was of considerable significance (Stetson 1928; Parrington 1958; Denison 1961; Ritchie 1964; Moy-Thomas and Miles 1971; Mallatt 1981). All authors are vague about the precise source of nutrition. More recently the importance of organic detritus as a source of food for filter feeders and sediment feeders has been realized (Sorokin 1981). Formed from the decaying remains of organisms, faecal pellets, and terrestrial organic material, these detrital



TEXT-FIG. 3. Longitudinal section of scroll coprolite, TCD 32417, from Louisburgh, Co. Mayo, Ireland. A, polished section of laminite containing the sectioned coprolite mounted in Araldite; the section shows the divisions between different whorls of faecal material extending the full length of the coprolite; surrounding the coprolite are patches of coprolitic material, $\times 3.3$. B, photomicrograph of the right-hand end of the same coprolite showing more clearly the parallel divisions between the 'layers' of faecal material, and the irregularly-shaped patches of coprolitic material beside the specimen, $\times 10$.

particles are the foci of microbial and heterotrophic activity (Fenchel 1970). They serve more as catalysts for energy conversion than as a direct nutrient source for sediment feeders (Conover 1978). The detrital cycle represents an active dynamic system, undergoing constant turnover (Finenko and Zaika 1970).

TEXT-FIG. 4. Drawings of longitudinal sections of three scroll coprolites: note that the divisions between adjacent whorls run parallel for the whole length of the section. A, TCD 32417, Louisburgh, Co. Mayo, Ireland, $\times 4.4$. B, T 3927, Birkenhead Burn, Scotland, $\times 5.7$. C, TCD 32412, Louisburgh, Co. Mayo, Ireland, $\times 7.8$.



The whole cycle is initiated with the introduction of freshly created organic material, from allochthonous and/or autochthonous sources (Sorokin 1978). Rapid colonization of these particles by microorganisms is followed by assimilation of the basic carbon structure of the detrital particle. This metabolism of the 'young' particle becomes less significant as the whole complex matures. The assimilation of dissolved organic matter now becomes of great significance (Khailov and Finenko 1970).

Grazing by protozoans and other members of the meiofauna stimulates bacterial productivity and therefore helps to maintain a high level of metabolism (Briggs *et al.* 1979). The complete detritus/microflora/meiofaunal complex is of great nutrient value (Odum 1970), supplying the protein, amino acid, lipid and carbohydrate requirement of detrital feeders (Parsons and Strickland 1962). Most detritivores do not possess the enzymatic ability to assimilate this material directly. They are therefore dependent on bacteria and fungi to convert the structural carbohydrate into an acceptable form (Briggs *et al.* 1979). Grazing by detritivores stimulates further microbial development by increasing the surface area available for microbial colonization by splitting particles, by resuspension of settled particles, and by the release of metabolites.

The small size of these particles is also significant. There is a peak of biomass available for particulate feeders among the smaller particle sizes (Conover 1981). The percentage of available carbon (non-carbonate carbon) in sediments also increases with an increase in the fine fraction (Zatsepin 1970). Since detritivores are in effect grazing the surface films of micro-organisms on these particles, selection in favour of fine particles will enhance the feeding efficiency and also increase the nutritional intake. Such selectivity is displayed by *Mugil cephalus*, the grey mullet, (Pandian 1975). Odum (1970) demonstrated a decrease in the percentage microbial coverage on detrital particles along the intestine of the mullet.

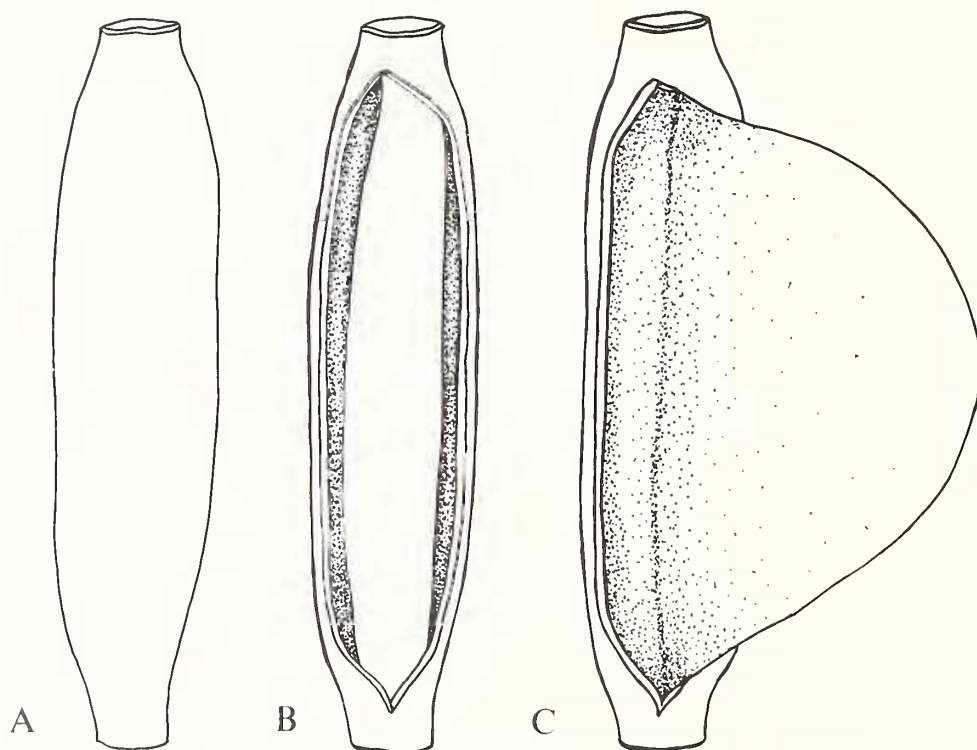
Organic detritus as a nutrient source is widely exploited today, especially by benthic invertebrates and a limited number of highly successful fish including: the milkfish, *Chanos chanos*; mullets, *Mugil* spp.; carp, *Cyprinus* spp.; and *Tilapia* (Odum 1970).

Members of all three invertebrate subphyla of the phylum Chordata – the Hemichordata, Tunicata, and Cephalochordata – feed on detrital particles. A recurring suite of features associated with feeding exists among these protochordates and also the early vertebrates: microphagy (feeding on minute particles), the utilization of mucus for trapping these particles, and the use of a perforated pharynx for filtering the particles. Initially simple filtration of these particles from the water column would probably have been sufficient to meet the nutrient requirements of these organisms. In addition to the above features some of these protochordates possessed a typhlosole (Fee 1925), which is an infolding of the intestinal wall resulting in an increased absorptive surface area.

Fee produced a table (1925, p. 183) showing the distribution of typhlosoles and valvular intestines among primitive vertebrates and fishes, and outlined the decline of such structures among more advanced fishes, concluding that the vertebrate line began with a tendency towards typhlosolar development in the intestine.

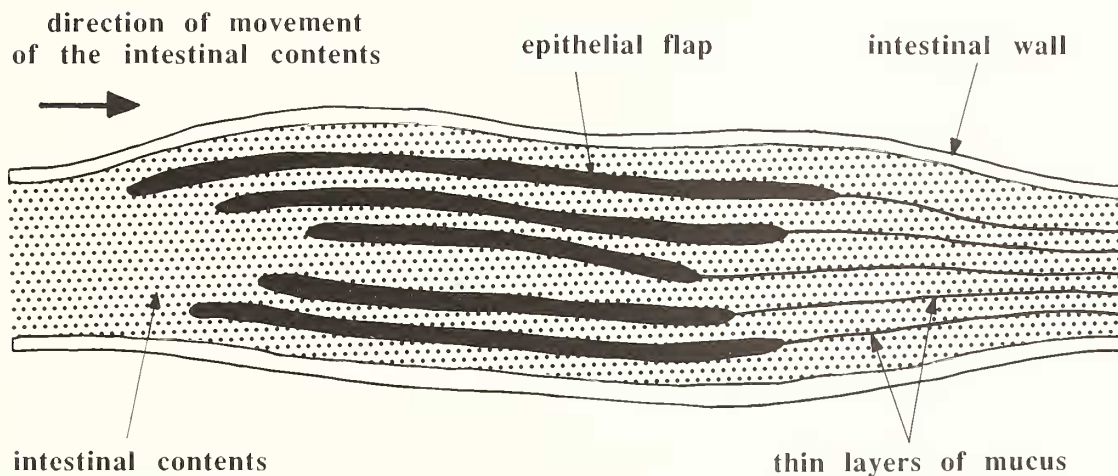
The list of fish groups possessing a valvular intestine includes elasmobranchs, holocephalans, dipnoi, polypterids, holosteans, acipenseroids, and the coelacanth (Fänge and Grove 1979). A reduced form occurs in the lampreys (Hardisty 1979). Fossil fish groups with evidence of valvular intestines are the placoderms, chondrichthyans and possibly acanthodians and actinopterygians (McAllister 1987). Its widespread occurrence testifies to its efficiency. The valvular intestine functions by providing an increased surface area and by slowing down the passage of material, both allowing increased absorption.

Two morphological types of valvular intestine exist, longitudinal or scroll, and transverse or spiral (Owen 1866). Embryologically both begin as simple elongate ingrowths of the intestinal mucosal layer into the lumen of the intestine, resembling a typhlosole. An epithelial flap develops and coils upon itself in the scroll valve, whereas in the spiral valve, the inner layer of the intestinal wall twists spirally around the longitudinal axis of the intestine as the epithelial flap develops, resulting in a more complex structure. As noted by Parker (1885), a huge range of variation occurs in the morphology of spiral valves. Fee (1925, p. 177) suggested that the scroll valve was the first to develop and that the transverse valve developed from secondary modification. The scroll valve which presently exists among some chondrichthyans may have subsequently re-arisen from a transverse type valve (Compagno 1988).



TEXT-FIG. 5. Diagrammatic representation of the dissection and unrolling of a scroll valve. A, intact valve. B, valve opened by a longitudinal incision, coiled epithelial flap visible inside. C, epithelial flap uncoiled and deflected to the right (after McAllister 1987).

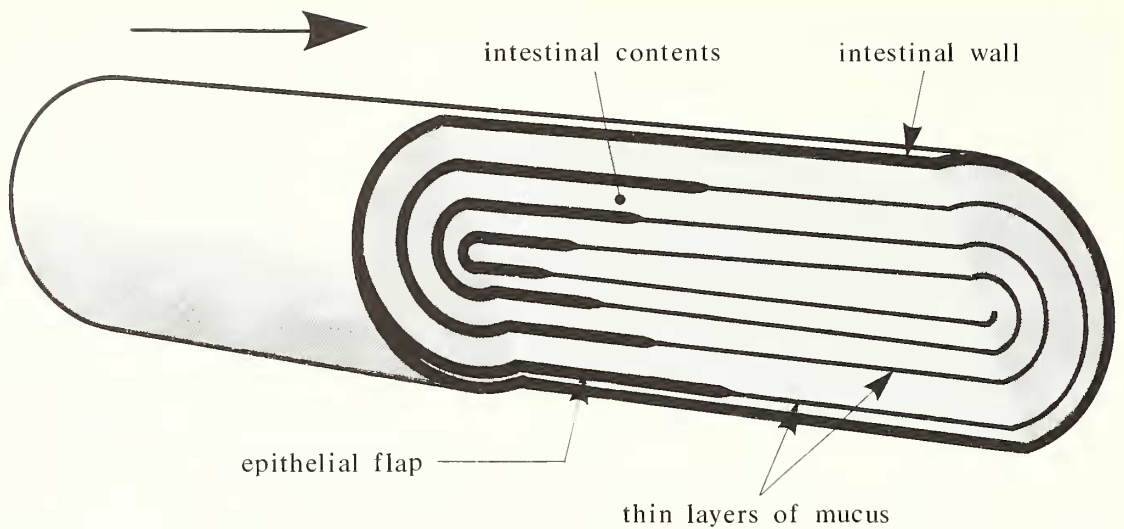
The production of solid faeces by the African lungfish *Protopterus annectans* was reported in 1903 by Bashford Dean. Jain (1981) described the faeces of an Australian lungfish, *Neoceratodus fosteri*. Initially upon expulsion both faeces display spiral structure which slowly begins to uncoil after a period in the water. This has obvious significance for the formation of spiral coprolites. Much of the disagreement in the literature about the formation of spiral coprolites centres on whether a coprolite represents fully extruded faecal material or is an intact valvular intestine packed with partially digested material. This evidence, along with observations by McAllister (1985) of spirally coiled 'cololite' material inside the colon of *Scyliorhinus canicula* (lesser spotted catshark), would seem to suggest that coprolites can represent fully extruded material. A packed valvular intestine, given the right circumstances, would also probably stand a high chance of preservation isolated from any body fossils.



TEXT-FIG. 6. Diagrammatic representation of a longitudinal section through a filled scroll valve. 'Layers' of material appear to become separated by thin layers of mucus as they exit the valve.

As described by Owen (1866) the scroll valve can be unrolled to form a flap of tissue (Text-fig. 5). In its naturally coiled form in the valvular intestine it has the effect of partitioning the intestinal contents. When viewed in longitudinal section the appearance is of discrete layers (Text-fig. 6). When viewed in transverse section the intestinal contents appear as a single continuous spiral coil. The principal direction of movement of the intestinal contents is parallel to the longitudinal axis of the intestine. So, as the material moves posteriorly, the valve terminates and the 'layers', beginning in the centre, come back into contact, separated only by thin layers of mucus. The function of this mucus is lubrication for the passage of the intestinal contents and protection of the epithelial wall. This results in a cylindrical coil of material similar to the coil in the valvular intestine without the epithelial flap (Text-fig. 7). Morphologically the scroll valve functions as a mould which imposes its shape on the material which passes through.

Not all the material passing through the intestine will maintain this spiral form. Only material of the correct consistency will reflect the form of the intestine (Zangerl and Richardson 1963). As these authors point out, information regarding normal faecal output of fish is lacking. It is therefore difficult to speculate as to whether the production of spirally coiled faecal material is the normal condition for fish with valvular intestines. Whether or not it is normal there appears to be an association between detritus, valvular intestines, and spiral coprolites. The scroll coprolites in the present study indicate that the organism responsible possessed a scroll intestinal valve and this represents the earliest occurrence of such a structure. The coprolites also suggest that detritus may have been one of the first major nutrient sources of the vertebrates.



TEXT-FIG. 7. Three-dimensional representation of a filled intestine containing a scroll valve. Diagram shows both longitudinal and transverse sections and the effect of the valve on the separation of the intestinal contents.

POSSIBLE PRODUCERS

The following organisms are the most likely candidates for producing the coprolites:

Agnatha: Anaspida; Cephalaspidomorphi; Heterostraci; Thelodonti.

Gnathostomata: Chondrichthyes; Placodermi; Actinopterygii; Acanthodii.

Others: Eurypterida; unknown faunal element.

A spiral valvular intestine has been proposed for the Carboniferous eurypterid *Cyrtoctenus wittebergensis* from the Witteberg fauna of South Africa (Waterston *et al.* 1985). The reported structure however lies at an angle of 90° to the longitudinal axis of the gastro-intestinal tract. The authors drew a comparison between the spiral structure they encountered and previously described amphipolar coprolites (Williams 1972). Williams, however, suggested that these coprolites originated from palaeoniscoid fish, which also occur in the Witteberg fauna. The proposed feeding methods of most eurypterids (Selden 1984), would not agree with the production of such finely particulate spiral coprolites.

The proposed feeding methods, based on tooth morphology, for the Palaeozoic Chondrichthyes all appear inconsistent with the production of such finely particulate coprolites (Moy-Thomas and Miles 1971; Zangerl 1981). Other evidence concerning food preferences comes from gastro-intestinal contents, gastric residues, and coprolites of Pennsylvanian age, all of which have been examined by Zangerl and Richardson (1963). They concluded that the sharks concerned were feeding mainly on other fish and arthropods.

The morphological adaptations of the earliest gnathostomes, the acanthodians (typical fusiform body, heterocercal tail, large eyes, grasping dentition, large gape), all suggest that they were nektonic and macrophagous and that benthic feeding was not a significant source of nutrition (Denison 1979).

A group with undoubted benthic adaptations is the placoderms. Dorsoventral flattening of the head and thoracic region, dorsal eyes, ventral mouth, and heterocercal tail all indicate this group's benthic mode of life (Denison 1978). From remarkably well-preserved specimens of the Upper Devonian *Bothriolepis canadensis*, Denison was able to determine much of the internal anatomy,

including an extensive valvular intestine. He also suggested that *Bothriolepis* ingested large quantities of detritus (Denison 1941). The first record of a placoderm comes from the lowest Devonian, the Gedinnian of Czechoslovakia and the Dittonian of Britain (Miles 1967), so although potentially capable of producing spiral coprolites it appears unlikely that they were responsible for the Louisburgh coprolites.

The Infraclass Actinopterygii is large and diverse and its members cannot be easily characterized. The first definite record occurs in the Lower Devonian (Schultze 1968), although Gross (1968) has assigned some isolated scales from the Upper Silurian to this group.

Our knowledge of agnathan anatomy and behaviour is still limited. The cephalaspids and the heterostracans, both ranging from the middle Ordovician (Denison 1967; Halstead 1988), display classic bottom-dwelling adaptations including dorso-ventral flattening, ventral mouth, dorsal eyes, and a heterocercal tail (Moy-Thomas and Miles 1971; Märss 1986). However, their absence from the impoverished fauna in Louisburgh would suggest that they were not responsible for the coprolites.

The impoverished fauna from Louisburgh consists of the spiral coprolites themselves, an anaspid agnathan *Birkenia elegans*, and thelodont scales (Palmer *et al.* 1989). The thelodont scales belong to the genus *Loganellia* (Turner pers. comm. 1990). Only a selection of the thelodont scales have been identified so it is possible that other thelodonts may also have had representatives in the Louisburgh fauna.

Thelodonts have 'not received as much attention as other agnathans' (Turner 1973, p. 557). They range from the Arenig Glauconitic Sands of Leningrad (Tarlo 1967) to the Middle Devonian (Ritchie 1963). The body form was a dorso-ventrally flattened cephalothorax and a laterally compressed trunk and caudal region. The tail was hypocercal and there were anal and paired flexible pectoral fins. The orbits were lateral, the mouth sub-terminal and ventral, and they possessed a sensory lateral line system. A body length of 100–200 mm is typical for thelodonts; however, some reached greater lengths, for example *Thelodus parvidens* around one metre (Turner 1986). Yet again the lack of information about the group has hindered any definite conclusions about the life habits of these agnathans. Opinions favour bottom feeding but there is also a possibility of some forms having been nektonic (Märss 1986).

The Anaspida are composed of mainly Silurian forms. They are the most fish-like of all the ostracoderms. Their laterally compressed fusiform bodies, reversed heterocercal (hypocercal) tail and elongate ventrolateral fins probably enabled the anaspids to be rapid and manoeuvrable organisms. Body size ranged from 50 to 300 mm (Halstead 1988), with most not exceeding 150 mm (Moy-Thomas and Miles 1971). Very little direct evidence of their feeding is available; the most common conclusion is that most were particulate feeders. Two anaspids, *Endeiolepis* and a new genus from Kerrera, as yet undescribed, display sedimentary infilling of the intestine (Ritchie 1964). This suggested to Ritchie that ingestion of sediment occurred during feeding.

Another possibility is that some unknown member of the Louisburgh fauna was responsible for the production of the coprolites. Such an organism would have to lack any preservable structure or not have encountered any favourable conditions for preservation, neither of which appears very likely.

From our original list of ten candidates we are left with the thelodonts (*Loganellia*) and anaspids (*Birkenia*) as the groups most likely to include the producer of the coprolites.

DISCUSSION

We know that the aquatic habitat in Louisburgh was probably relatively shallow with low current velocities and anoxic bottom conditions (Maguire 1989). The locality of the water body was within the tropics, and probably in the Southern Hemisphere (Märss 1989). It is not clear exactly what proportion of their lives some of these earliest vertebrates spent here. This habitat may have represented a migration route, a feeding area, a nursery, or perhaps the entire lifecycle occurred here. What appears certain is that the defaecation occurred here or upstream. X-ray diffraction

analysis revealed no compositional difference between the laminites and the coprolites. The implication of this is that the organisms producing the coprolites were ingesting the detrital material which made up the benthic deposits. Of course the final position of the coprolites in the laminites may or may not be close to the feeding site. The coprolites could have either been deposited directly into the laminites as the fish swam over or they could have drifted in if they were sufficiently buoyant (Trewin 1986). The lack of any consistent orientation of the coprolites on the bedding surfaces would suggest that if they did drift they were under the influence of weak or inconsistent currents.

The lack of work on the whole subject of faecal output of modern organisms removes a potentially useful source of information. We can only speculate whether the production of spirally coiled faeces by organisms possessing valvular intestines is a normal or an abnormal occurrence. The production of such spirally coiled faeces would appear to be a coincidental by-product of the shape of the intestine, because it is difficult to imagine any evolutionary benefit to an organism with such an ability. There is also difficulty in interpreting what exactly the measured length of the coprolite represents. Is it the length of the scroll valve? Or the length of the rectum where the coprolite may have spent a brief period before being expelled? Or possibly a combination of both?

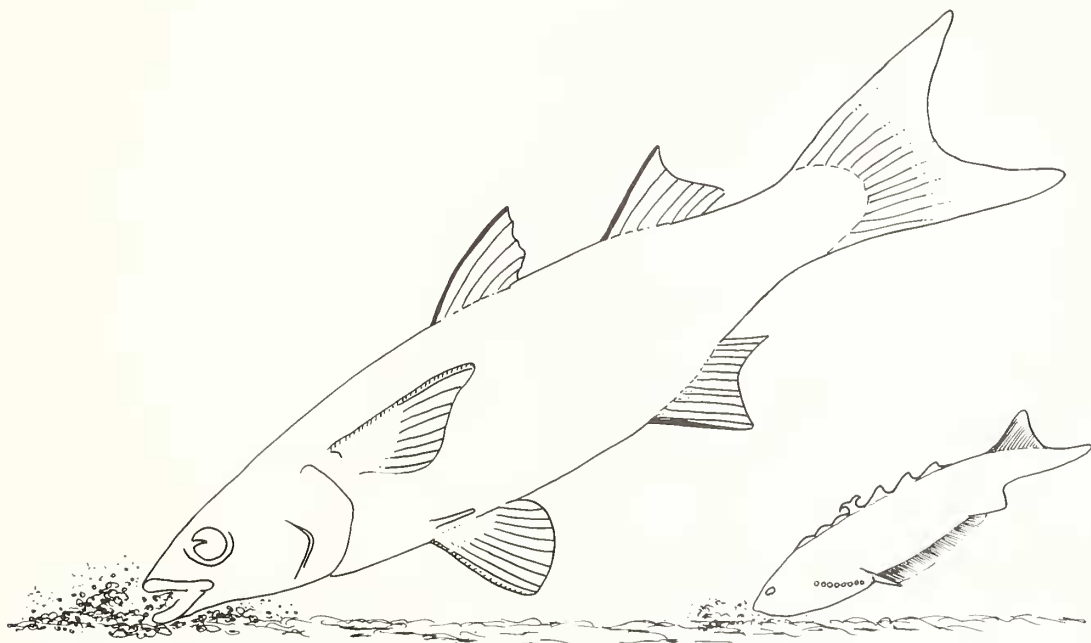
A likely evolutionary sequence can be traced from relatively simple hemichordates through organisms of increasing complexity to the early vertebrates. A recurring suite of features can be followed through this sequence. These features are all associated with particulate feeding and include a filtering pharynx, ciliary and/or muscular pumps for generating feeding currents, the involvement of mucus in the entrapment and transportation of the particles, and an intestine structurally adapted to give an increased absorptive surface area.

Detritus has been demonstrated to be a significant nutrient source for such organisms. As the size and complexity of the organisms increased it was necessary to develop increasingly efficient particulate feeding methods. The increased complexity and mobility which characterized the vertebrate grade allowed a more successful exploitation of detritus as a nutrient source. Within this context the agnathans were the first vertebrates to achieve dominance. The exact phyletic relationship of the Agnatha and the Gnathostomata is as yet uncertain. Their staggered occurrence in the fossil record leads to the general assumption that the agnathans were ancestral. More recently they have been interpreted as sister groups (Hardisty 1979). For the agnathans to achieve this initial domination, in abundance at least, it may have been necessary for them to have had some competitive advantage. I would suggest that, limited as they were to microphagy (Halstead 1982), agnathans were able to expand more rapidly by the continued exploitation of detritus as a pre-existing nutrient source. The gnathostome's ultimate competitive advantage, the acquisition of jaws, required more time for refinement. Indeed the morphological adaptations which can be discerned from agnathan fossil remains appear to concur with this idea. The striking similarity they show to modern detritivores (Ritchie 1963), the discovery of organic-rich sediments in the intestines of some specimens, and now the discovery of these coprolites, all point to the fact that particulate feeding was of significance for early vertebrates.

The existence of spiral coprolites in association with these organisms is not incongruous. Vertebrates began with a tendency towards typhlosolar development of the intestine (Fee 1925). The increased absorptive area of the intestine is a feature which is associated with feeding on detrital sediments, due to the ingestion of large proportions of nutritionally impoverished material (Kapoor *et al.* 1975). The morphology of the coprolites gives us firm evidence that their producer possessed a scroll intestinal valve, whose function was to allow an increase in the uptake of nutrients.

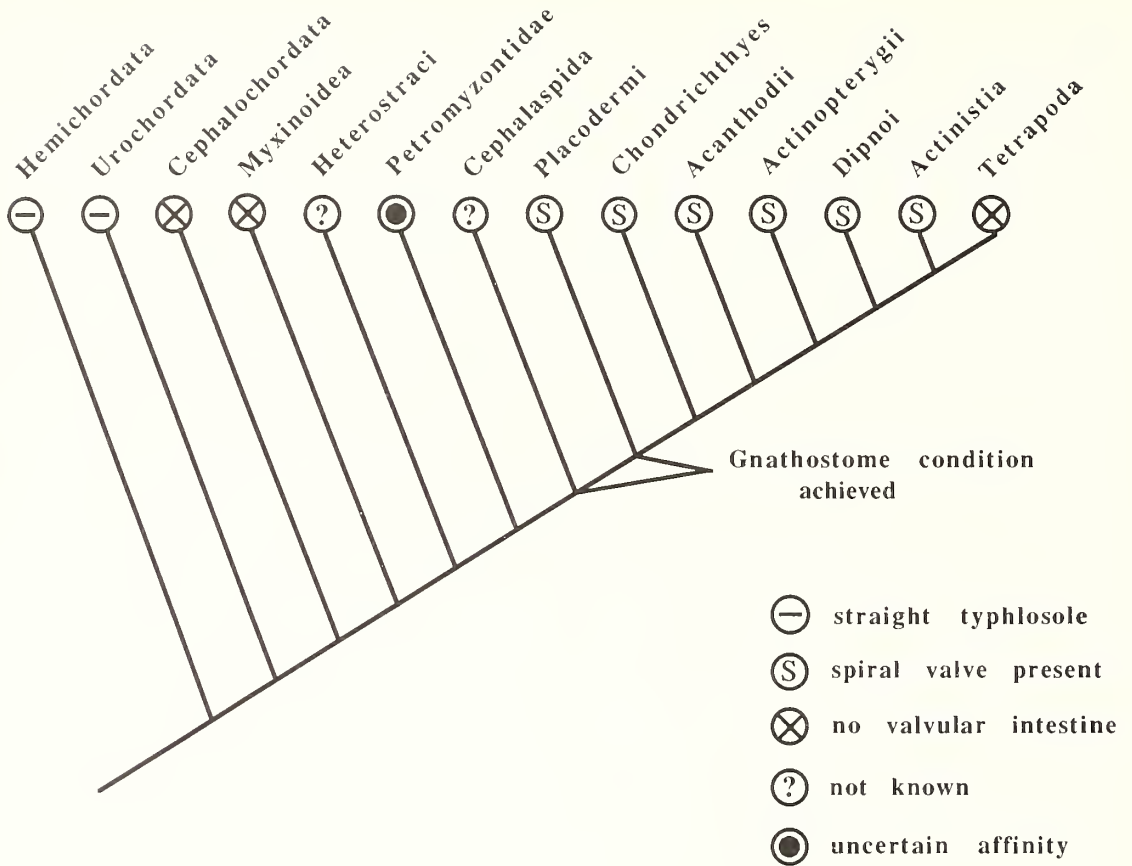
The fine-grained composition of the coprolites relative to the texture of the matrix indicates the occurrence of some degree of selection or filtration. This particle selection/filtration is most likely to have occurred prior to ingestion since this removes the requirement for any major morphological adaptations of the buccal and pharyngeal cavities to produce a complex sieving mechanism. No evidence of such a mechanism has yet been discovered. Pre-ingestional selection of small particles also avoids causing damage to the delicate gill membranes. We know that flexible areas, indicated by a covering of minute scales, were present in the cheek regions of *Birkenia* (Simpson 1988). This flexible buccal region may have been involved with 'blow-suction' feeding as employed today by the

mullet (*Mugil cephalus*). Variation in the time between the blow and the suction phases could effectively regulate the size of particle ingested, the finer material taking more time to re-settle. This is an attractive feeding model since it agrees with both Parrington's (1958) and Janvier's (1987) proposed feeding angle for the anaspids, and may allow feeding without causing bioturbation. No feeding marks have been identified from the laminites. Alternatively a 'soupy' sediment/water interface would also allow detrital feeding while preserving the settled layers below. It is possible to imagine *Birkenia* swimming above the substrate, periodically inclining its body at an angle so that its mouth is close to the sediment, and feeding in such a fashion (Text-fig. 8). An interesting point which may hold some significance is that, inclined at such an angle, the slanting row of gill openings becomes more or less horizontal to the substrate. Mentioned earlier was the probable existence of anoxic bottom conditions in Louisburgh. Therefore such a periodic method of feeding may have been associated with the requirement for an adequate uptake of oxygen.



TEXT-FIG. 8. A comparison of the feeding angles of the mullet, *Mugil cephalus*, (left) and that proposed for the anaspids (right) by Parrington (1958) and Janvier (1987).

The terminally placed mouth of *Birkenia* would have required such an angled approach to benthic feeding. The mouth position of *Loganellia* is thought to have been ventral, just behind the anterior margin of the head, resulting in a horizontal feeding angle. The relative size of the eyes of both organisms indicates potentially divergent approaches to feeding. The larger laterally placed eyes of *Birkenia* may possibly have allowed a more selective approach to feeding and indicate that visual stimuli may have been important. In contrast the eyes of thelodonts usually only appear as small darker stains in the general area where eyes would be expected (Ritchie 1963). Their dorsal situation would prevent visual stimuli from having an important role in food selection. This does not necessarily mean that thelodonts were unselective feeders – they may have possessed other sensory mechanisms involved in food selection, such as sensory barbels as displayed by modern benthic feeding catfish.



TEXT-FIG. 9. Cladogram showing the distribution of typhlosoles and valvular intestines among protochordates, the main fish groups, and tetrapods. Compiled from Fee (1925), McAllister (1987), and with the assistance of Dr Alain Bleick.

The respective size range of the *Birkenia* and *Loganellia*, relative to the coprolites, gives no firm indication as to which was the producer.

When we examine the known distribution of valvular intestines (Text-fig. 9), it appears that the possession of a spiral valvular intestine may in fact be a gnathostome feature, which has been subsequently lost among the tetrapods. Youson (1981) is convinced that vertebrate valvular intestine is not homologous with the structure present in the intestine of the lamprey. Thelodonts, based on scale morphology, may in fact be a sister group of Palaeozoic sharks and so have gnathostome affinities (Turner pers. comm. 1990). If this link can be established it would then strengthen the case for these coprolites being of thelodont origin.

Probably the most satisfying conclusion would be the ability to identify with certainty the organism or organisms responsible for producing the scroll coprolites. The scarcity of evidence reduces the certainty with which such a conclusion can be made. The almost total lack of preserved body fossils and the poorly understood lifestyles of the organisms involved contrive to conceal the identity of the producers. However, these coprolites indicate that the scroll valve was the most primitive type of valvular intestine. They also point to the importance of detritivory among some of the early vertebrates.

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